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THE PHYLLOTAXY OF PHOENIX CANARIENSIS

By Cornelius Beach Bradley

Date palms of this species are frequently grown as ornamental trees in and about Berkeley, California. They are mostly young trees that are approaching maturity or have recently attained it. As the leaves grow old and bend low toward the ground, they are generally lopped off to get them out of the way, leaving the stumps however in place on the trunk. Since these stumps persist for years, they build up in time an authentic record of the development and arrangement of the leaves, complete save where accident or decay has marred it, and save also that it does not include the earliest period of growth; for through the enormous expansion of the trunk during that stage, all the earliest leaves are torn from their attachments and lost long before the regular trimming of the leaves begins. This record of the leaf-stumps was found to be of very great assistance in working out the phyllotaxy of the tree, and is frequently cited as "the record" in the discussion which follows.

I

1. A preliminary survey made it evident that the problem here presented is not by any means the simple one usually encountered in a study of this kind, namely, the deciphering of a single and a stable pattern, and the identification of it with one of the "regular" patterns described in the textbooks. On the contrary, all the ordinary clues were here completely lost in a maze of uncertainty caused by constant change of pattern. Only at a single point between infancy and maturity was there a pause where the wheeling ranks stood still long enough to be counted. Never before had the writer encountered anything of this sort, nor from

his early reading of the authorities could he recall so much as a suggestion that such things ever occur.* Here then was a challenge which could not be ignored or neglected.

2. After careful examination of many specimens it became clear that each tree of this species has passed through several distinct phases of phyllotaxy, namely: (1) The initial pattern of infancy, not included in the record, and at this stage not yet identified, but later found to be of the 5-ranked pattern (cf. Chart, Zone I). (2) At an uncertain distance above this the record begins in the midst of a zone of no recognizable pattern whatever, because it offers no vertical alignments to form the basis of a numbered scheme (cf. Chart, Zone II). (3) Near the upper edge of this zone, out of what is apparently mere confusion, there presently emerges a recognizable group of oblique spiral ranks which, curving sharply upward, presently reach verticality. There are thirteen of these ranks—so now we know where we stand, though not as yet just how we got there (cf. Chart, Zone III). (4) This vertical alignment sometimes continues unchanged through a space of several feet. Quite as frequently, however, the thirteen ranks merely touch verticality and then gradually swerve away from it. But in either case they do not lose themselves in confusion like that from which they emerged at first.* For here the 13-ranked pattern in its entirety is visibly carried forward along these curves without dislocation or change, save that the whole is slightly tilted in conformity with their deflection (cf. Chart, Zone IV). (5) This gradual rotation of the pat-

* In the writer's student days the botanical authorities within his reach had very little to say concerning deviations from the regular series of leaf-patterns except as the deviations were the result of seasonal changes in the growth of the plant, or of modification of leaves to subserve new functions. Since then it has not been possible for him to follow up the later developments of phyllotactic theory. While acknowledging the seriousness of this handicap for the present task, he still ventures to think that in one way this may not have been wholly a disadvantage—it has at least left him free from theoretical bias to deal with the facts as he found them.

* This double curve of the 13's, with its two arms meeting in Zone III, is the most noticeable feature of the whole record and a valuable landmark for the investigator. Its curvature is always convex toward the direction of the primary spiral. Cf. Section III, 3 *infra.*

tern presently brings into play a new alignment of thirty-four vertical ranks, forming a pattern familiar to Californians in the cones of *Pinus Sabiniana* and *P. Jeffreyi* (cf. Chart, Zone V). For a long time no further change was discovered beyond this point.

3. The appearance of fruit at this stage marks the attainment of maturity, and since during this portion of the study no indication of further change appeared, it was tentatively assumed that the 34-ranked pattern was final. Not until after the study was supposedly complete and the paper was actually in the Editor's hands, did the writer discover that in a few older trees the bending to one side of the thirteen ranks is carried beyond the point at which the 34-ranked alignment becomes vertical, being continued in some instances until the 55-ranked scheme is passed, and the 21-ranked scheme is reached. Whether this is or is not the final scheme, cannot yet be affirmed. Meantime it has not been thought necessary to reconstruct the Chart or to discuss the matter further here.

II

Thus in the phyllotaxy of this tree there are seen to be at least five distinct phases, namely: three of well-known "regular" patterns, while two different groupings of leaves showing none of the recognized alignments occupy the intervals between them. Leaf-development, however, is perfectly continuous throughout the whole series; nowhere is there node or break of any sort. Each of the undescribed arrangements grows directly out of the pattern below it, and grows directly into the pattern above it. Obviously these are organic transformations. What is the essential factor in the process, and how does it work out these changes?

1. In all these patterns, regular and irregular alike, four elements are absolutely constant, namely: (*a*) The primary spiral of growth; (*b*) its direction, left or right; (*c*) the axis about which it coils; and (*d*) its division into equal parts by applying to it a constant unit of measurement, namely, the circumferential arc of 360 degrees, or one turn about the axis. The only other

element in the whole system is the leaf-interval, or rather the interfoliar arc; for it is not a linear dimension measurable on the surface, but an arc measured by the angle at the center. This arc thus becomes a second unit of measurement applied to the primary spiral along with the other. When these two arcs are commensurable, by virtue of their coincidence at regular intervals, they gradually build up those systems of vertical ranks by which we recognize the "regular" patterns. Each of these has its own dimensions of arc, and only so long as the dimension remains constant is the pattern identifiable.

2. Our transition zones then are areas in which gradual change in the interfoliar arc operates to rearrange one of the regular patterns, building up out of it the transitional formation, and out of that again the next regular pattern of the series. What at first seemed to be mere disorder and confusion, turns out to be a marvel of order and symmetry when once its method and structure are understood.

3. Let us assume that the primary spiral is a right-hand one like that in the chart. Any increase of the leaf-interval will set each successive leaf a little beyond—*i.e.*, to the right of—the place where it would otherwise have been. If the increase continues, it will presently cause the vertical ranks of the pattern to swerve visibly to the right—toward the direction of the primary spiral. On the other hand, any diminution of the interval will set each successive leaf a little behind—to the left—of what would otherwise have been its place; and the vertical ranks will then swerve to the left, or away from the primary spiral. In either case all the other alignments of the pattern will be similarly affected, though in less degree the further they are removed from verticality. The whole pattern thus undergoes a sort of rotation to right or to left as the case may be; and this, if continued, will gradually swing into verticality some one or other of the ranks which were secondary spirals of the original pattern. Whenever the predestined secondary rank thus becomes vertical, further change in the leaf-interval is brought to an end as we have seen, and the transformation is complete. The whole proc-

ess may be followed in detail in sections II and IV of the Chart. If the primary spiral were a left-hand one, all of these features would of course be reversed.

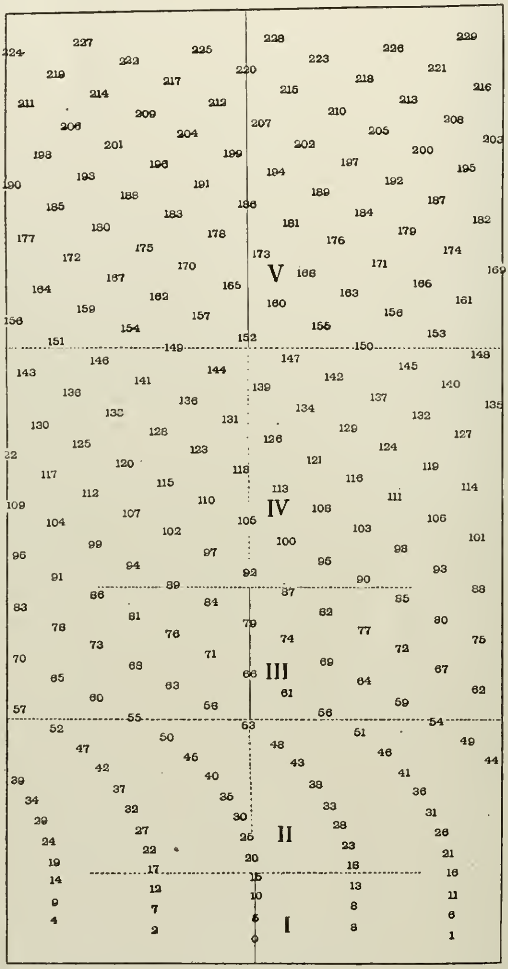
4. The actual amount of change in the interfoliar arc required in order to accomplish these transformations is astonishingly small. The dimensions of the arcs of the three regular patterns with which we are here concerned are given—as fractions of the circumference—in the very formulas by which we distinguish them, namely, $2/5$, $5/13$, and $13/34$. The change required to accomplish the first transition is therefore the difference between the first and second of these fractions; and to accomplish the second, the difference between the second and third. Reduced to decimal form these fractions become 0.400, 0.3846, and 0.3823; and the differences are 0.0154 and 0.0023—the latter amounting only to three fourth of a degree of arc, or one seventh of the minute-interval on the face of a watch. Yet this infinitesimal quantity must be subdivided and distributed over perhaps half a hundred leaf-intervals! *De minimis curat Natura.*

It may seem difficult to account for decrease in the interfoliar arc while the girth of the tree is rapidly increasing. But greater girth simply means larger surface for the insertion of more leaves; and in the case of an endogenous and branchless tree like our palm, it is imperative that no space be wasted—that the growing leaves be crowded together as closely as they can be made to stand. Such being the case, so long as increase in girth keeps ahead of the demand for foot-space for larger leaves, the record will indicate that fact in a changing pattern; because even a constant space on an increasing circumference subtends a diminishing angle at the center. If demand for foot-space catches up with increase of girth, that fact will appear as a pause in the shifting ranks. If increase again gets ahead, change will begin again. If finally equilibrium is established, the pattern reached at that point becomes permanent, and with it the interfoliar arc. Such in brief seems to be the explanation of the strange metamorphoses we have been watching.*

*Among later theories concerning changes in leaf-patterns to which the writer's attention has been kindly directed by the editor of TORREYA, the one

III

The actual sequence of the various parts of this study can perhaps be best understood by following a brief detail of the construction of the Chart.



1. After drawing throughout the field of the Chart the lines of a right-hand primary spiral as the basis of further operations,

which most nearly approximates in its calculated results to the scheme actually presented in our Phoenix is Weisse's Mechanical Theory of Transition, in Goebel's Organography of Plants, translated by Balfour, 1900, Vol. I, p. 74 *ff*.

the thirty-four vertical ranks and the right- and left-hand secondaries of Zone V were plotted at the top. Below this—but with a gap between left for the as yet undeciphered transition—there was made a similar plot of the thirteen-ranked Zone III. These were the only portions of the record so far positively identified and understood. All else was uncertain.

2. The bridge between these two was obviously the next thing to attack. For not only were both its abutments already in place, but the whole record of its construction was there in plain view on the trunk of almost every adult tree of its kind, though as yet we could not read it. All attempts however to devise a scheme which should result in a pattern at all like that of the record were unavailing, until at last the significance of the increasing pitch of the 13-ranked secondaries as they curve downward from Zone V was apprehended.* They curve in order to meet and merge themselves tangentially in the vertical ranks of Zone III. After that it was not difficult to discover the right curve and to plot the girders which were to connect the abutments of the bridge. Leaf-stations then were marked throughout the three zones, and lines of provisional numbering were established as basis for the final numbering of the whole when the plot of Zones I and II should be completed. Thus plotted, the result was not only intelligible, but—what was far more important—it actually represented what was seen in the record of the tree.

3. There still remained Zones I and II. By this time it had been ascertained that the leaf-pattern of the first is 5-ranked, and that it lasts but a very short time before passing into the transition of Zone II. So a narrow zone of that pattern was plotted at a suitable distance below Zone III, and the transition was accomplished precisely as it was in Zone IV above—by bringing down the 5-ranked secondaries of III on a curve which finally merged them in the verticals of Zone I. Leaf-stations were then plotted throughout these two areas, and permanent numbering was established throughout the Chart.

4. The reader of course will not imagine that the broad open

* See in Plate I the descending curve between Nos. 190 and 112, and in Plate II between Nos. 148 and 96.

spaces of the lower portion of the Chart represent at all what would be actually seen on the stem of the infant tree. At the beginning of its growth the five ascending leaf-ranks, instead of being widely separated as shown in the Chart, stand in actual contact about the slender stem—and continue so throughout the life of the tree. The problem of the Chart, however, is not one of dimension, but of alignment; and for that, Mercator's projection has the great advantage of representing all lines of *constant* direction as *straight* lines on a plane surface, and not as conical or conoidal spirals, which all of them save the verticals actually are.

Within the limits of this short paper it has not been possible to attempt more than a demonstration of the fact and the method of orderly phyllotactic transition from one of the established patterns to another. The many and larger questions which grow out of this study must await further study.

Note.—Concerning these the writer will be glad to receive suggestions from any one interested in these matters. His address is 2639 Durant Ave., Berkeley, Cal.

Explanation of the Plates.

Plate I. *Phoenix Canariensis*, with right-hand primary spiral—clean-shaven below and with fruit-clusters appearing above among the leaves. All traces of Zones I and II have perished, save that a few leaf-scars from the upper edge of II are still visible just at the surface of the ground (Nos. −8, −13, −5). These are the upper ends of 13-ranked secondaries curving sharply upward from the transition zone below to become the vertical ranks of Zone III. Rising obliquely right and left are the 8-ranked and the 5-ranked secondaries, the former having the steeper pitch. At the level of leaf 52 the vertical ranks began to incline toward the left, as they enter the transition of Zone IV; causing the grade of the 8's to become a little steeper, and that of the 5's to become less steep, as the rotation progresses. At the level of leaves 164–169 the transition comes to an end, and the 34-ranked regular pattern begins so that leaves 198 and 203 stand vertically above the two last named.

Plate II. *Phoenix Canariensis*, with left-hand primary spiral, reversing all the alignments of Plate I, and showing a much lower section of the record than is commonly preserved—Zones II (in part), III, IV, and the lower edge of V. The great curve of the 13's is strikingly shown in its continuous form, without pause at verticality in Zone III, and convex toward the left, turning at about the level of leaves 101–104 into the transition of Zone V. Within the crown of leaves, above, Nos. 161 and 156 may be seen vertically placed above Nos. 127 and 122. Zones III and IV are here much more condensed than in Plate I.